The Form and Functioning of the Pallial Organs

in the Opisthobranch *Akera bullata*

with a Discussion on the Nature of the Gill

in Notaspidea and Other Tectibranchs

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(7 Text figures)

IN THE DISPOSITION OF THE ORGANS of the mantle cavity and the structure of the gill, the shelled opisthobranchs have long been known to present deep-seated differences from the prosobranchs. In many respects, the tectibranch gill stands well apart from the broad path of branchial evolution in Mollusca as a whole. This was clearly recognized by YONGE (1947) in leaving aside the opisthobranchs from his broad general study of the molluscan pallial cavity. No full account has yet been published of the adaptations and workings of the pallial organs in those opisthobranchs once grouped together as the "Tectibranchia." The following description of the anaspidean *Akera bullata* Müller, 1776 is now offered as a contribution to that end. Although, as was long ago shown by GUIART (1901) and more recently confirmed by MORTON & HOLME (1954), *Akera* is clearly a generalised aplysiomorph with a coiled external shell, the condition of the mantle cavity lends it to a useful comparison with the bullomorphs.

In both the Cephalaspidea (Bullomorpha) and Anaspidea (Aplysiomorpha), together making up the order Pleurocoela, the mantle cavity has undergone partial detorsion. It no longer opens forward, but faces outwards towards the right side, and is sited far back in the posterior half of the body. The head shield and foot of the cephalaspids, and the naked body of the aplysiids have supplanted it as the dominant structural unit. So long, however, as the mantle cavity survives at all as a working component in the opisthobranchs, it continues to draw in water anteriorly from the environment well to the front of the animal. This is a feature of leading importance in the orientation of the prosobranch body (MORTON, 1958), being facilitated there by the post-torsional forward posi-

tion of the inhalant pallial opening. In *Akera* the functional effects of partial detorsion are delayed by the siting of the effective entrance to the pallial cavity at the side of the head, in the space enclosed by the right parapodium (Figure 1). A current of similar strength passes also beneath the left parapodium. The chemoreceptive Hancock's organ, lying in the rhinophoral groove below the headshield, is thus as strategically placed to sample the inhalant water current as was the prosobranch osphradium that it has functionally replaced. A similar anteriorly placed inhalant opening may be noted in the primitive and fully shelled bullomorph *Ringicula* (see FRETTER, 1960). Here the parapodial margin is raised up in the anterior mid-line to form a small median inhalant siphon (Figure 5). During shallow submergence in the sand, this maintains effective contact with the water above ground level.

Even with the full loss of the enclosed mantle cavity, the Notaspidea (Pleurobranchomorpha) preserve effective anterior and posterior openings to the space occupied by the gill plume (see Figure 7). In *Umbraculum* the plume is partly overhung by the mantle underlying the shell, and is bounded below by the expanded foot. In pleurobranchoids, such as *Pleurobranchus membranaceus* (Montagu, 1811) (Figure 6), the gill space can be partially enclosed from above by the flexible edge of the notum and from below by the foot. Far from "emancipating" themselves from any disadvantages of torsion, the gilled tectibranchs would appear – in conserving the anterior site of pallial entry – to be delaying as far as possible the full effects of its loss.
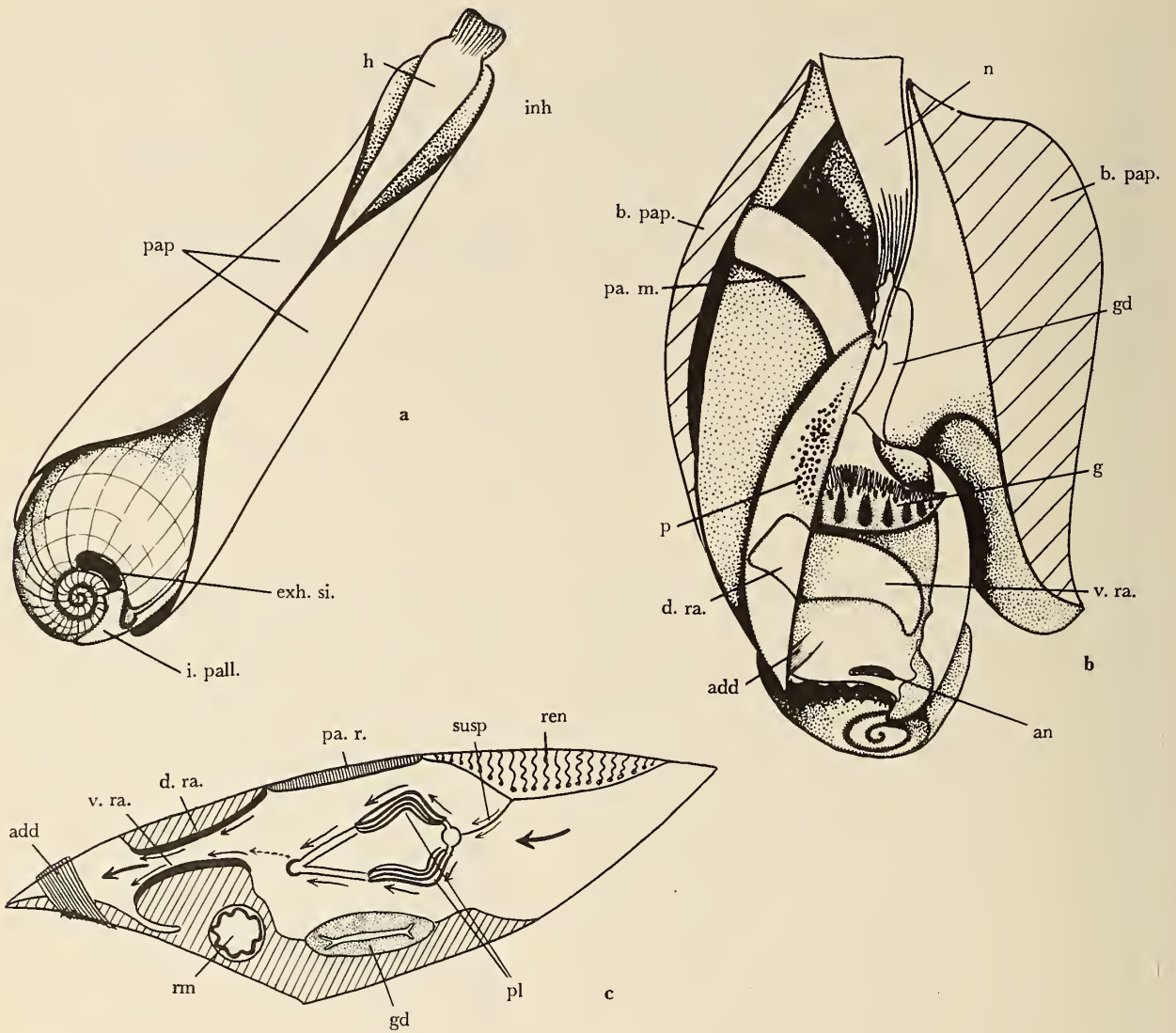
Figure 1

Akera bullata

a. The intact animal fully extended, showing the parapodia folded over the shell, and the entry and exit points of the water current.

b. The visceral and pallial region as exposed by cutting away the parapodia and partly reflecting the margin of the mantle to show part of the gill and raphe.

c. Schematic longitudinal section of the pallial cavity.

add – posterior adductor muscle   an – anus

b. pap – cut bases of the parapodia   d. ra – dorsal raphe

exh. si – exhalant siphon   g – gill   h – head

gd – female genital duct   inh – inhalant site

n – neck connecting head with visceral region

i. pall – infrapallial lobe   p – purple gland

pa. m – pallial margin   pap – parapodia   pa. r – pallial roof

pl – plicae of gill   ren – renal organ   rm – rectum

susp – suspensory membrane of gill   v. ra – ventral raphe

After drawing aside the dorsally overlapping parapodia (Figure 1b), the immediate pallial opening of *Akera* appears as a long narrow slit running the length of the shell aperture. It is closely bounded by two lobes of the mantle skirt, a thinner suprapallial lobe, widely reflected over the sharp outer lip of the shell, and a wider and more fleshly infrapallial lobe extending over the bulging body whorl below. In the natural state of the parts the thin margin of the infrapallial lobe extends up to embrace the suprapallial lobe and the effective openings of the pallial cavity are thus restricted to either end of the slit. The inhalant passage lies in front where the body is well ensheathed by the right parapodium, and the exhalant opening faces directly backwards. The path of water through the pallial cavity is thus transverse to its long axis and anteroposterior with reference to the whole animal. Looking from behind at an animal with the shell intact (Figure 2c), it can be seen that the suture line of the body whorl is incised so as to leave a narrow rectangular cleft, the so-called exhalant siphon. This aperture is guarded by the pallial tentacle, and opens directly in the wake of the crawling animal. The anus lies immediately at its threshold. On drawing away the suprapallial lobe, the infrapallial lobe is seen to be drawn out behind into a backward directed gutter, richly ciliated over its whole lining. Beneath its floor the rectum is usually discernible by the sandy texture of its contents.

The pallial organs may be further revealed by cutting away the thin lip of the shell and further drawing back the suprapallial lobe (Figure 1b). At the extreme border of this lobe a zone of ciliated cells maintains a current beating away from the pallial cavity. Immediately within the cavity, the suprapallial lobe is studded with a zone of darkly opaque, purplish brown subepithelial glands. These correspond in position and histology to the purple gland of *Aplysia* and they produce in *Akera* a similar purple secretion.

The pallial cavity (Figures 1c, 2a) contains two principal sets of organs, a pair of broad, flat, strongly ciliated tracts, the dorsal and ventral raphe, leading into a short pallial caecum; and immediately in front of these tracts a transversely placed plicate gill. The ventral raphe terminates in a backward-curved extension, upon the infrapallial lobe, just within the inhalant siphon. The dorsal raphe lies immediately opposite to and above it upon the pallial roof. In their natural relations upon the roof and floor they enclose only a narrow slit between them. With their broad faces close together, they run backwards to lie upon the upper and lower wall of the caecum, which is a narrow, somewhat tapering outgrowth applied to the surface of the last whorl of the visceral mass. It corresponds to the similar structure represented in vari-

ous bullomorphs, where it is often not incorporated in the visceral mass. Thus *Scaphander lignarius* (Linnaeus, 1758) has a free, shortly coiled pallial caecum. *Actaeon tornatilis* (Linnaeus, 1766) (see FRETTER & GRAHAM, 1954) (but apparently not all Actaeonidae [Rudman, personal communication]) has a long narrow caecum of several whorls, coiled independently of the visceral mass, and resting in the furrow between the whorls.

Further forward in the pallial cavity lies the gill, running parallel with the terminal section of the raphe outside the caecum (Figure 2a). When fully relaxed the gill projects slightly from the mantle cavity with its pointed tip a little recurved. It is horizontally attached along its whole anterior (efferent) edge by a wide, smooth suspensory membrane, which secures it to the front wall of the mantle cavity. The posterior (afferent) side is attached at its base only, by a much shorter suspensory membrane. Along the free posterior edge of the gill runs a large afferent blood vessel, and the anterior margin is traversed by the efferent vessel.

The gill (Figure 3) appears to be constructed of narrow folds or leaflets arranged both above and below its horizontal axis. Here all resemblance to the bipectinate ctenidium of Archaeogastropoda ceases, for the details are highly distinctive. The basic structure of the gill is that of a double fold of integument reaching horizontally across the mantle cavity. There is no distinct axis with a skeletal support, the whole interior of the fold being a wide blood-space. The gill acquires its surface complexity by the throwing of its expanse into deep convolutions, forming transverse folds repeated from the attachment to the tip. These folds have their greatest development along the anterior margin, where they are produced into fan-shaped tufts of small plicae. At this edge, the efferent blood vessel has a more or less direct course, becoming a little sinuous as it drains tufts of plicae alternating on the upper and lower aspects of the gill. Each cluster of plicae appears to divide soon after its origin into three or sometimes four moderately separate portions, each containing about 10 - 12 separate folds. The anterior (efferent) margin of the gill is scalloped when viewed from the edge (Figure 3b); each cluster of plicae rises more or less steeply to a low summit, sloping away more gently towards the posterior edge of the gill. Here the clusters are connected by wider stalks to the afferent vessel running along the posterior margin. Each cluster has the appearance of a radial sheaf of folds, springing from its basal stalk.

The impression of distinct tubular vessels is however deceptive. Apart from the continuous double fold of integument, blood-filled throughout, there are no vessels at all. In a longitudinal section, the "stalk" vessels of tufts
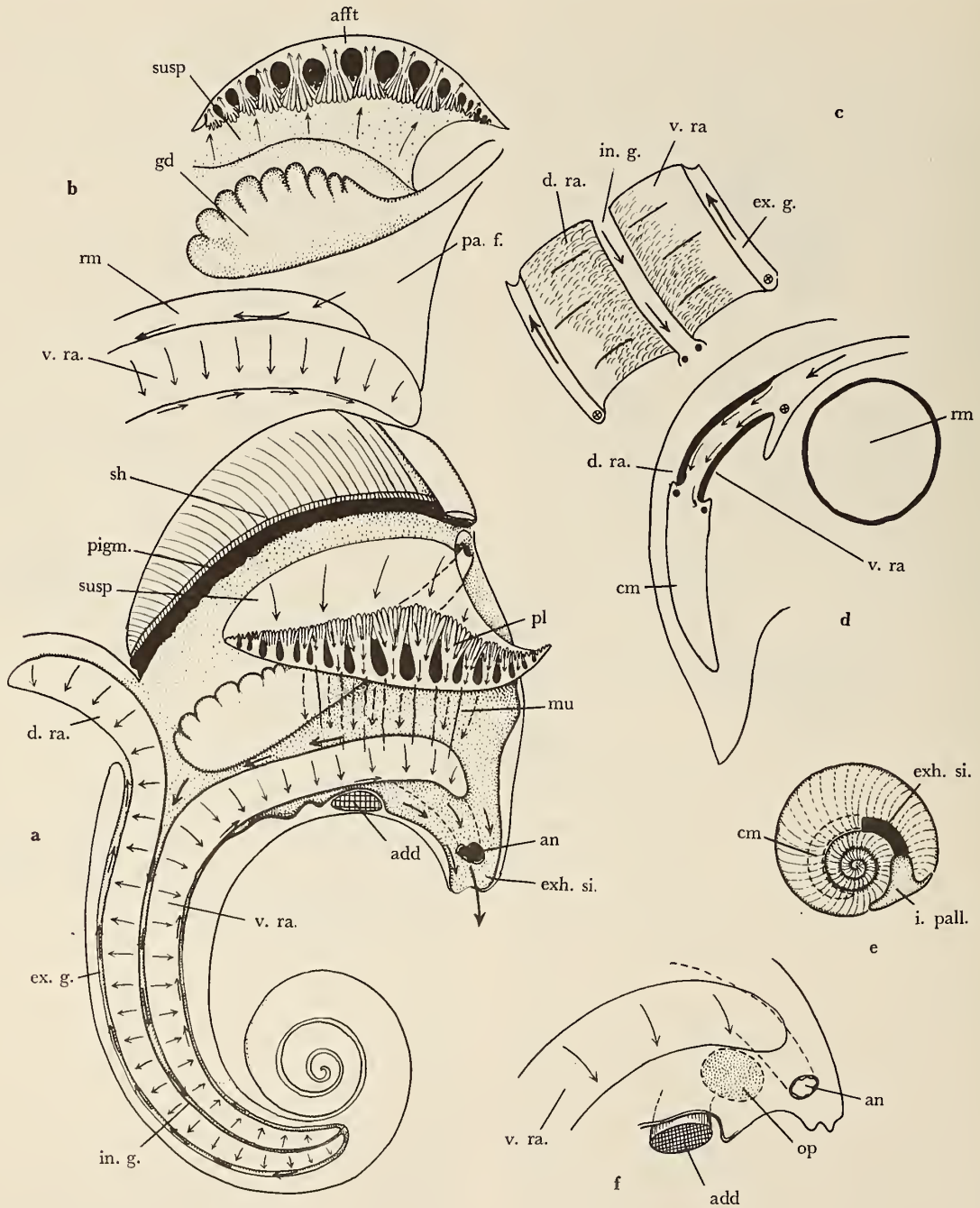
Figure 2

Figure 2

(← on facing page)

Akera bullata

a. The pallial cavity and caecum laid open to show the gill and the complete course of the dorsal and ventral raphe.

b. The gill drawn forward attached to its suspensory membrane, showing the adjacent ventral raphe and female genital duct.

c. A small portion of the caecum, showing the incurrent and excurrent grooves.

d. Transverse section of the pallial caecum and rectum.

e. Posterior view of the shell, infrapallial lobe and exhalant 'siphon', with the extent of the pallial caecum indicated in broken line.

f. The relation between the anus, adductor muscle and extremity of ventral raphe.

add – posterior adductor muscle   afft – afferent margin of the gill
an – anus   cm – pallial caecum   d. ra – dorsal raphe
    ex. g – excurrent groove   exh. si – exhalant siphon
    gd – female genital duct   in. g – incurrent groove
   mu – mucus strings drawn from the gill to the ventral raphe
i. pall – infrapallial lobe   op – opaline gland   pa. f – pallial floor
pigm – pigmented outer surface of mantle   pl – plicae of the gill
sh – cut edge of the shell   susp – suspensory membrane of gill
      v. ra – ventral raphe

Figure 3

(above)

Akera bullata

a. Distal portion of the gill, viewed from the anterior (= efferent) margin, showing the alternating dorsal and ventral tufts of plicae, with their ciliary currents.

b. Surface view of part of the gill, showing the tufts of plicae and their origin from the so-called "afferent vessel" along the posterior edge.

c. and d. Camera lucida drawings showing the construction of the plicate gill, towards the base of a plical tuft (c) and distally (d). The inset sketch (e) shows the access of water currents at either side of three alternating tufts of plicae.

    aff – afferent vessel   bl – undivided vascular space
d – dorsal surface   i. pl – interior of double integumentary fold
      pl – plicae of gill   v – ventral surface
     vasc – vascular base from which plicae arise
       w – water-filled space between plicae

are seen to represent merely the summits of a continuous set of folds. The leaflets of the plicae are themselves constructed in the same way, by producing a continuous fold alternately on either side into a sheaf of minor folds (Figures 3c, d). A consequence of this structure is that water can never pass, as between ctenidial filaments, from one side of the gill to the other. Instead, the respiratory current has access on either side of the gill to the labyrinth of spaces where gaseous exchange can take place. The cleft between two tufts leads however only to the inside face of the alternating tufts of the opposite side (Figure 3).

The gill itself is capable of a certain muscular movement, perhaps helping to promote water movement between the plicae. But the creation of the pallial water current has devolved in *Akera* upon the ciliated tracts of the dorsal and ventral raphe. The plicae of the gill have no such well-defined ciliary tracts as the filaments of the prosobranch ctenidium. The surface of each plica maintains however a weak cleansing current, carrying particles up the anterior face, over the summit and down the posterior surface. The direction of ciliary transport and water flow is thus – as in the prosobranch ctenidium – the reverse of the direction of blood flow. Posteriorly directly ciliary currents pass across the suspensory membrane towards the gill itself.

There is in *Akera* no specialized ciliated epithelium upon the gill, the tufts of cilia being short and scattered upon isolated single cells or groups of cells incorporated in the thin, low-celled respiratory epithelium. Along the summits of the plicae, cilia are most closely distributed (Figure 3e).

The narrow blood space within the plicae is crossed by connective trabeculae between the membranous walls. The basement membrane incorporates slight amounts of smooth muscle, but no supporting skeletal rods are developed, and the whole gill has only the rigidity given by the efferent and afferent vessels. In fixed material, goblet cells were not often seen, but the gill's total production of cleansing and binding mucus must be considerable; particles of carmine and carborundum are quickly wrapped in mucus and carried down the posterior face of the gill for disposal off the afferent edge. From here the gathered mucus strings are engaged by the much more powerful cilia of the ventral raphe and drawn across in thick ropes towards the surface of this tract.

The best comparison with the histology of the gill plicae, with their incorporation of unspecialised patches of cilia and goblet cells, is to be found in Pott's clear account of the fine structure of the circumanal gills in *Onchidoris fusca* (MÜLLER, 1776) and *Archidoris pseudoargus* (Rapp, 1826) (POTTS, 1966).

The macroscopic structure of the gill of the larger *Akera soluta* (Gmelin, 1791) was early described and figured by PERRIER & FISCHER (1911). Its chief differences from *A. bullata* lie in the subsequent convolution of the whole length of the gill, by which the number of plical tufts is greatly increased. Using the same system of construction, there is a secondary complexity here that *A. bullata* has never attained.

To pass to the dorsal and ventral raphe, each of these tracts in *Akera bullata* is a smooth strip of tall-celled epithelium, thicker than the surrounding integument, and provided with cilia of great length and power, beating posteriorly across the breadth of the raphe. These cilia produce the antero-posterior flow of pallial water and their pattern of metachronal beat can be clearly observed with a binocular microscope, persisting for many hours after the dissection and display of the caecum.

The caecum is wide and shallow, and only a relatively small part of its roof and floor are occupied by the dorsal and ventral raphe (Figure 2a). The anterior edge of the ventral raphe overlaps forward, partly to overhang a broad furrow, continuing from the floor of the mantle cavity up to the tip of the caecum. Up this tract beats a strong ciliary current into the caecum. Against the posterior edge of the ventral raphe runs a similar but much shallower groove conveying a downward current, continuous with the upward current after passage round the tip of the raphe at the extremity of the caecum. Throughout the caecum the cilia of the raphal surfaces beat backwards, across the tract. The principal flow of water is thus between and across the raphes, being drawn directly across the gill in its passage through the mantle cavity. The important subsidiary current, that travels up the caecum, appears to carry a load of particles progressively diminishing, since the strong raphal cilia give the particles an oblique motion and draw them across the raphe for more direct expulsion.

The histology of the two raphes is identical, their epithelium consisting of wide, brick-shaped columnar cells. Each bears a ciliary tuft, as much as 50μ long, but occupying less than a third of the free surface of the cell. A well-developed intracellular fibrillar apparatus descends to the cell base on one side of the nucleus. In fixation the cilia are grouped together in coherent tapering bundles. From the appearance of the living cilia, and the clarity with which the working units appear under low power, it appears that the cilia of each cell may beat together as a single whip (Figure 4b).

The pallial caecum occurs widely in the "tectibranch" order Pleurocoela. In the Anaspidea (Aplysiomorpha) it appears in *Akera* but evidently not in the Aplysiidae,
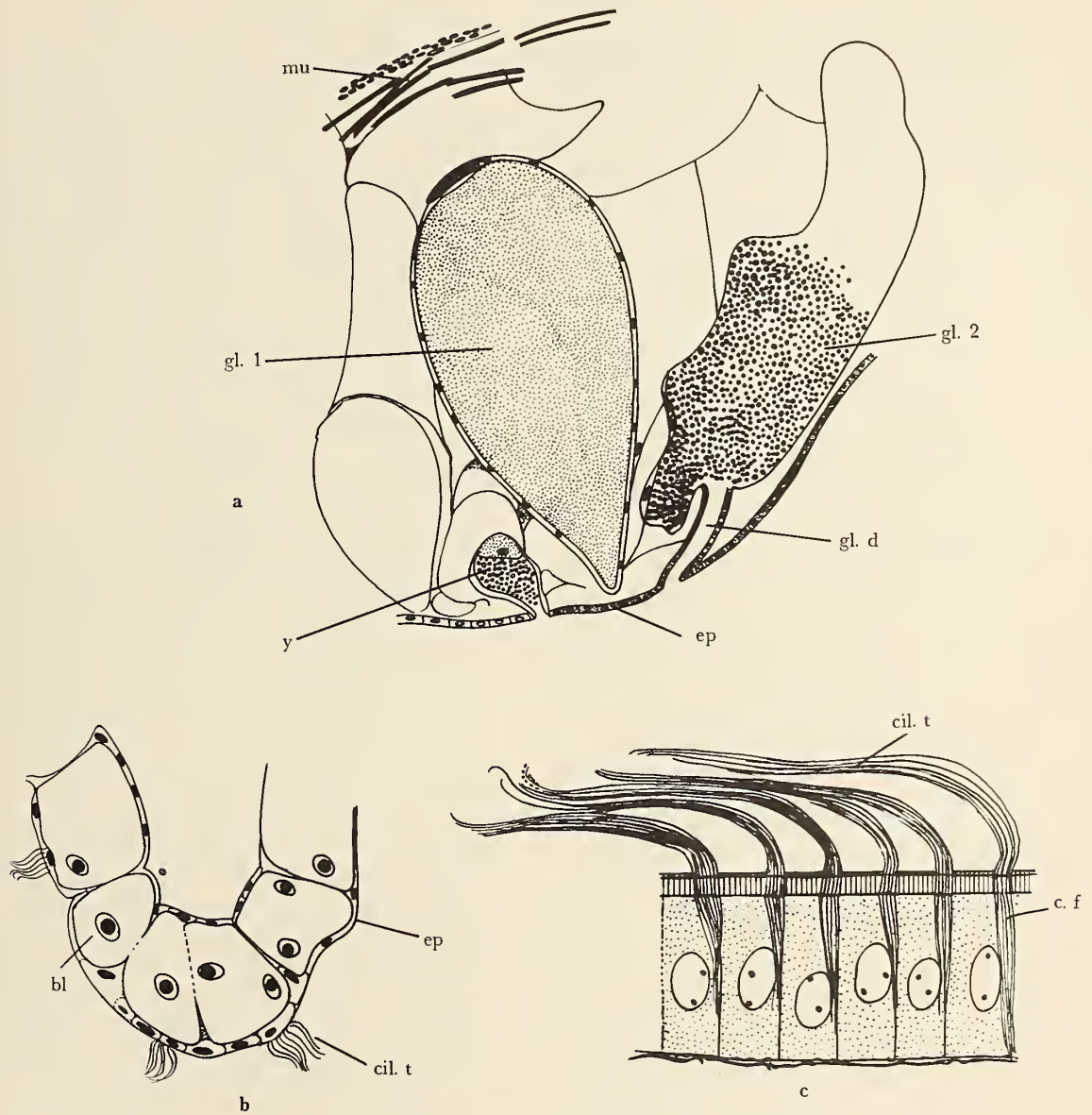
Figure 4

Akera bullata

a. A group of cells from the purple gland.
b. Transverse section of portion of a gill plica.
c. Ciliated epithelium of a raphe of the pallial caecum.

cil. r – ciliary bundle of raphal cell
cil. t. – ciliary tuft of respiratory plica

bl – blood cell   c. f. – intracellular ciliary fibrils

ep – simple lining epithelium   gl. d. – duct of large gland

cil – ciliary tuft of gill epithelium

gl. 1, gl. 2 – the two types of large purple gland cell

mu – muscle fibres at base of gland cells   y – young gland cell

which have suffered further simplification of the mantle cavity. In the Cephalaspidea (Bullomorpha) the caecum finds its best expression in the long, independently spiral prolongation of the mantle cavity of certain Actaeonidae (FRETTER & GRAHAM, 1954). The functions of this organ have been briefly discussed by Fretter and Graham, while for *Akera* and several species of bullomorphs PERRIER & FISCHER (1911), give a general morphological account. The caecum may well be an ancient heritage of the pleurocoeles as a whole, its degree of development varying with ecological conditions. It appears to have a special adaptive importance in those forms living in turbid waters or upon a soft substratum, particularly those burrowing beneath the surface.

The caecum has generally been credited with a cleansing function, as in *Actaeon tornatilis* where it may form a long flushing siphon circulating a clean water current that keeps the pallial cavity clear of inborne sediment. Such a current with its long, inward and outward circuit has been described as respiratory, but the caecum has no unusually developed vascular supply, while the integument of the gill is itself folded into a seemingly ample surface for gaseous exchange. The most tenable view is that, with the shifting of the function of current production to free the whole gill surface as a respiratory area, the dorsal and ventral raphes exhibit a tendency, with frequent parallels in other molluscan ciliary systems, to enlarge their active area by prolongation into a spiral caecum.

In the simple mantle cavity of the thecasomatous pteropod *Limacina,* a pronounced inward and outward water circulation has been described within the mantle cavity, probably in connexion with ciliary food collecting (MORTON, 1954). There is no gill and no special development of raphal tracts.

A special feature of the mantle cavity of *Akera* is the development of what may be called anterior and posterior adductor muscles, running directly between the free, somewhat flexible lip of the shell and the surface of the adjacent body whorl. These muscles appear to arise as detached slips of the columellar muscle, which runs back from its origin in the foot as a broad strap, radiating out of its columellar insertion beneath the pallial cavity floor. The anterior adductor muscle is placed just beneath the genital aperture, well in front of the afferent suspensory membrane of the gill. The posterior adductor lies at the extreme posterior end of the mantle cavity, inwards from the anus and some distance clear of the ventral raphe. Its function is evidently to narrow or partly close the aperture, by adducting a still somewhat flexible part of the shell-lip against the body whorl.

This adductor muscle strongly recalls the single muscle in the same position in the primitive shelled sacoglossan *Cylindrobulla* (Evans, personal conversation and unpublished notes). Here the most recently formed lip of the shell is highly flexible and can be drawn against the body whorl to close the aperture almost completely when the animal is withdrawn.

An ultimate stage in the evolution of such an adductor muscle may well be shown by the extraordinary sacoglossan *Tamanovalva* described by KAWAGUTI & BABA (1959). This is a "bivalved gastropod," representing an opisthobranch with a hinged, two piece-shell adducted by a single central shell muscle. A minute coiled visceral spiral is present at the apex of the right valve, which is by presumption the original univalved shell. The left valve, attached by hinge and adductor muscle might have arisen from a separate center of calcification developed within a flexible and adductible shell lip.

The histology of the purple gland of *Akera bullata* is illustrated in Figure 4a. There are two cell types, as present also in the prosobranch hypobranchial gland; but the purple gland differs, as in all Anaspidea, from a hypobranchial gland in having its gland cells entirely subepithelial. On topographical grounds it could best be regarded as a separate acquisition in the "tectibranch" mantle cavity. The gland produces a dense purple secretion, held for *Aplysia* to be a dibromindigotin (see COMFORT, 1951), wafted out of the mantle cavity as a protective and perhaps repellent screen. The prosobranch hypobranchial gland would appear to be more unequivocally represented as suggested by FRETTER & GRAHAM (1954) for *Actaeon tornatilis,* in the gland cells found in the pallial caecum of that species. In *Akera* no such specialised cells were observed, and a clear homologue of the hypobranchial gland would be difficult to establish. In *Akera bullata* an opaline gland, producing a repugnatorial secretion, lies in the infrapallial lobe, vertically below the purple gland in the intact mantle cavity. Its gland cells, with those of the purple gland, have been histologically described by PERRIER & FISCHER (1911) for *Akera soluta.*

COMPARATIVE DISCUSSION

The older literature gives a wealth of general description of the variant types of opisthobranch gill, almost all of it superficial in its attention to fine structure. HOFFMANN (1938) would recognise as basically comparable structures all the gills represented among Cephalaspidea, Anaspidea and Notaspidea, leading finally to the central
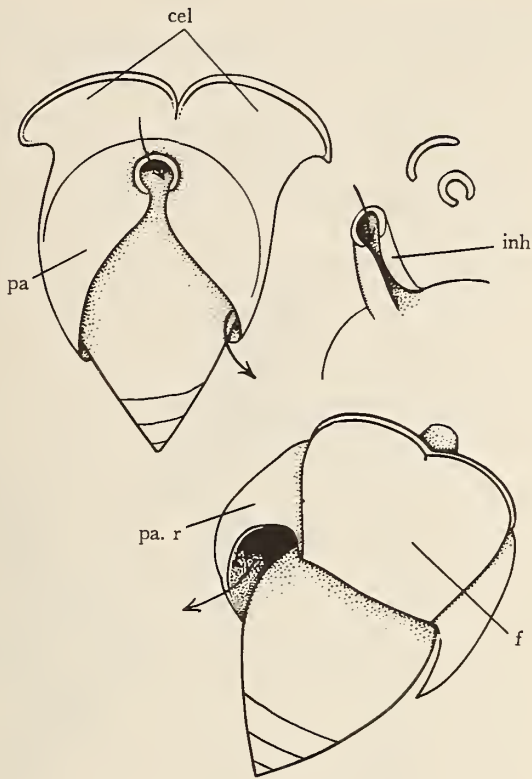
Figure 5

Ringicula buccinea

a. Animal viewed from above showing the pallial inhalant siphon.
b. The siphon in side view, with cross sections showing its change of shape.
c. Animal from below, showing exhalant site, on the right side of the body.

ce l – cephalic lobes   f – sole of foot   inh – inhalant siphon
pa – parapodia investing shell
pa. r – right parapodium with exhalant site

perianal gills of the dorid nudibranchs. The finest account of the form and ciliation of the nudibranch gills is given by POTTS (1966) for *Archidoris* and *Onchidoris*.

None of these opisthobranch gills can properly be likened to a ctenidium. As the widely represented gill among chitons, prosobranchs, bivalves (and, with modification, in cephalopods) the ctenidium has a set of very well-marked characters. In the generalised condition, that may be typified by the Archaeogastropoda, the bipectinate ctenidium has two opposite rows of triangular thin-walled filaments lying side by side as parallel leaves. These have always a characteristic ciliation, with current-driving lateral cilia, and cilia along either margin (frontal and abfrontal) generally carrying particles for rejection to the apex of the filament. A pair of chitinous skeletal rods run through the filament beneath the epithelial tract of the lateral cilia, and may give special support against the strong vibratory strain in this area. They must also stiffen the filaments to keep them narrowly apart as a comb or a grid, through which water passes and against which suspended particles are filtered out. As fully demonstrated by YONGE (1947) the homologies with the more specialised ctenidial filaments in other molluscan classes and even with the muscular ctenidium of the cephalopods are very clear.

In its relations with the heart and pallial circulation, and – in Pleurocoela – its position in the mantle cavity, the opisthobranch gill would show a reasonable topographic correspondence with a ctenidium. But as soon as its detailed structure and functioning are examined, it becomes clear that it has undergone a very special evolution upon its own lines. This gill is purely a respiratory organ, entirely relieved of the current-producing role of the ctenidium. Whatever its particular pattern of folding, the opisthobranch gill forms histologically a double fold of thin epithelium, with scattered mucus goblet cells and groups of ciliary cells, sometimes concentrated towards the margins, or otherwise freely dispersed. Freed from the stereotyped requirements of the ctenidium, the opisthobranch gill has been able to exploit a more plastic form-range than is found among all the rest of the Gastropoda.

Among the early shelled opisthobranchs, the only resemblance to true ctenidial filaments would appear to be the parallel leaflets of the primitive oxynoacean Sacoglossa. The genera *Oxynoe* and *Arthessa* can be regarded in many respects as the most prosobranch-like of the Opisthobranchia (Evans, unpublished observations). They can also from the outset be set apart as the earliest level of the clear-cut sacoglossan series, one of the most distinctly segregated lines of the opisthobranchs. In the Oxynoacea, the ciliation of the gill leaflets is however diffuse and patchy, the cells having little regularity of pattern. There are no powerful or localised lateral cilia, nor any skeletal rods.

Pleurocoela. In those bullomorphs, *Haminoea* and *Scaphander*, about which we have most information, we find a plicate gill structure recognisably comparable with that of *Akera* (Figures 6a, b). The respiratory surface of the gill is carried between two straight marginal blood vessels, forming along either margin a frame slung by a suspensory membrane. The whole expanse of the respiratory surface is thrown into transverse plicae. These are
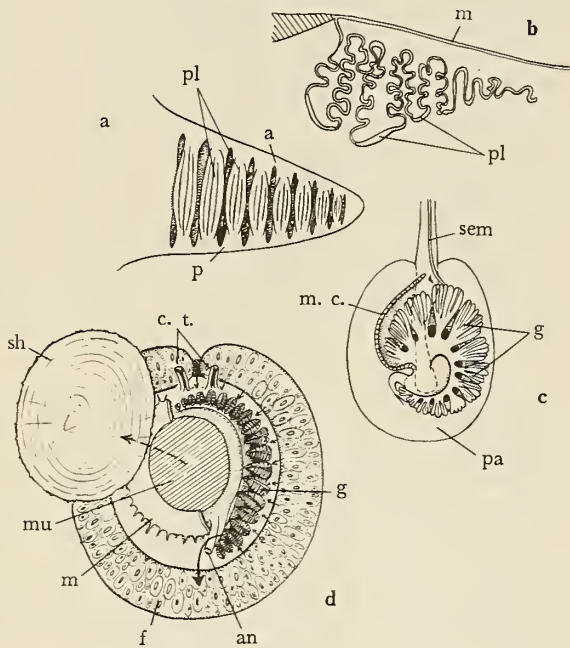
Figure 6

a. A bullomorph gill in schematic surface view, and
b. in longitudinal section, showing the folding into plicae.
c. The form and extent of the gill in the aplysiomorph *Dolabella agassizi* (modified from MacFarland, 1918).
d. *Umbraculum sinicum* with shell removed and mantle cut away on right side to display the gill.

a – anterior margin of gill   an – anus   c. t – cephalic tentacles
f – sides of foot with papillae   g – gill   m – mantle
m. c – cut edge of mantle   mu – shell attachment muscle
p – posterior margin of gill   pa – parapodial region opened out
    pl – plicae of gill   sem – seminal groove

not produced into radial tufts, but are gathered up into a parallel series of pleats, forming a repeatedly folded ruff, lying in the flat plane of the gill. The plicae are apparent from the surface as narrow-edged transverse folds, separated by deep fissures that incise the body of the gill.

The gills of the highly primitive *Actaeon* described by Fretter & Graham (1954) and of the small and generalised *Newnesia antarctica* E. A. Smith, 1902 appear also to be of this same type. For *Gastropteron* the freely projecting gill is illustrated by Guiart (1901) as produced into long and separate triangular pinnae, each convoluted by small transverse plicae running across its width. The gill of *Hydatina* (Perrier & Fischer, 1911) which appears to be plicate at its anterior edge like that of *Ha-*

minoea is frayed out posteriorly into pinnae of the *Gastropteron* type.

The aplysiomorphs or Anaspidea appear in general to have a gill structure closely agreeing with *Akera* (Figure 6c). The tufted gill of *Aplysia* is of this type, as is also that of *Dolabella agassizii* (MacFarland, 1918) and of *Notarchus glaucus* (Cheesman, 1878) as briefly investigated during this study. With the "sea hares" as distinct from *Akera*, there is a tendency for the plicate gill to outgrow the mantle cavity, its tip frequently projecting and the whole axis being arranged crescentically around the anterior and right aspects. The histology and structure of the plicae seem to present few differences from *Akera*.

Notaspidea: (Figure 7). The Notaspidea (Pleurobranchomorpha) or "side-gilled slugs" have a prominent external gill persisting on the right side, after the final abolition of the pallial cavity. The more primitive condition is found in the Umbraculidae, of which *Umbraculum sinicum* (Gmelin, 1791) was briefly examined in the course of the present work. A plate-like external shell surmounts the notum. The shell and pallial margin overhang a space where the gill curves crescentically around the right side of the shell muscle. Its anterior half, lying beneath the front of the shell, is attached by two suspensory membranes, attached on the outer and visible side to the efferent blood vessel, and on the concealed inner side of the afferent vessel (Figure 7). The posterior half of the gill projects freely back as a plume, with no suspensory membrane at the outer side.

Of the naked, slug-like Pleurobranchidae, with a vestigial subnotal shell, *Pleurobranchaea novaezelandiae* Cheesman, 1878 and *Pleurobranchus membranaceus* have been examined in life. The whole gill lies laterally, and tapers backward, with no suspensory membrane visible at the outward edge. In their account of the structure and biology of *P. membranaceus*, Thompson & Slinn (1959) make only brief mention of the gill, which can now be given a somewhat fuller description. Plume-like and bipectinate, it is built upon an antero-posterior axis, attached over its anterior two-thirds to the right body wall. The space containing it is bounded and able to be temporarily enclosed by the overlap of the notum and the thinly prolonged margin of the foot. A tubular pseudo-pallial space can thus be established, with its principal entrance in front and an improvised "exhalant siphon" formed by the crenation of the posterior edge of the notum (Figure 7). Within the same space, immediately in front of the gill, lie the anus, renal pore and genital apertures. Also in front of the gill is the "pre-branchial gland" or so-called "poison gland," of uncertain homology but perhaps comparable with the aplysioid opaline gland.

The gill axis projects horizontally from the body wall. Along its mesial edge runs the afferent branchial vessel, with the efferent vessel upon the exposed lateral edge. In

Figure 7

The gill of *Oscanius membranaceus*

a. The intact animal from the dorsal surface, to show the relation of the gill plume to the notum and the foot.

b. A group of gill pinnules, to show the ciliary currents and direction of water flow.

c. Schematic transverse section of the gill, showing axial blood vessels, and two pinnules in face view.

a – gill axis   af – afferent vessel of gill   c. te – cephalic tentacles

exh – exhalant side formed by embayed notum

ef – efferent vessel of gill   f – foot   g – gill in situ

lc – ciliary tracts on lateral surface of pinnule

lr – ridges on lateral face of pinnule

m – smooth membrane at inner edge of pinnule

mu – mucus string along lower edge of pinnule

n – notum   pa – ciliated papilla at base of gill pinnule

o – outer edge of pinnule with terminally directed ciliary currents

sh – position of shell indicated by transparency

vel – velum

its position and circulation the pleurobranch gill has a general resemblance to that of the bullomorphs, but its detailed structure is obviously different. Above and below the axis springs a row of pinnules, diminishing in length posteriorly. Those of opposite sides alternate, and at the outer base of each pinnule is a short, bluntly tipped papilla. Each pinnule has the form of a narrow triangular lamella compressed from side to side and thickest at its exposed edge. Its sides are covered with short close-set plicae, running across the width, with a slight inclination towards the pointed apex. The inner or mesial edge of the pinnule is continued into a smooth suspensory membrane, attaching the pinnule to the gill axis for up to a third of its length. The exposed margin of each pinnule is covered with small divergent corrugations carrying cilia that drive a weak current to either side. Particles then travel down the groove between the lateral plicae. There are no distinct lateral cilia nor is any water current maintained comparable in power to that of the prosobranch ctenidium or the pleurocoele pallial caecum. Passage of particles along the lateral grooves seems to serve a purely cleansing role. Mucus strings of bound sediment accumulate alongside the suspensory membrane of the pinnule. These are carried distally until the lamellae become free of the membrane, after which collected waste is discharged from the pinnules or between their tips. The papilla at the base of each pinnule is clad with fine, distally beating cilia (Figure 7).

Binding and cleansing mucus is freely produced by the epithelial glands of the gill. As in *Akera* and other Pleurocoela, the respiratory integument has little responsibility for current production. In *Pleurobranchus* the current through the peribranchial space is not a strong one. Water circulation can be best promoted, or excessive or harmful sediment removed, by the free movements of the parapodia, particularly by the intermittent swimming, described for *Pleurobranchus membranaceus* by THOMPSON & SLINN (1959).

Nudibranchia. The gills of the nudibranch sea slugs still await a published survey, much of which will be supplied when definitive results are presented from the valuable work of POTTS (1966). The two sorts of gill structures include the series of lateral tufts of the Tritoniidae, including *Tritonia hombergi* Cuvier, 1802 (THOMPSON, 1962) and the circumanal gills of the Doridomorpha, which may vary from simply pinnate to elaborately branched. An instructive transitional stage is that of *Bathydoris* (EVANS, 1914) with the gill and anus still lying at the right side. The plume-like form of the gill would seem to point to a clear homology between pleurobranchomorph and normal doridomorph states.
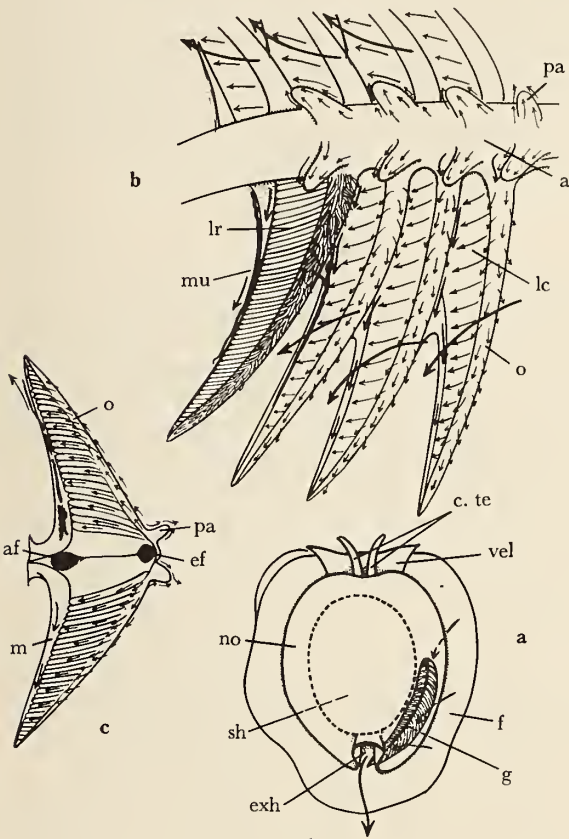
The present results establish the wide variety of gill structures that in Opisthobranchia replace the standard structure of the prosobranch ctenidium. Whatever its subsequent homologies among the dorid nudibranchs may be found to be, the pleurobranchoid gill has little detailed resemblance to the gill of the Pleurocoela. With the eventual emancipation from the shell, the sea-slugs have a high capacity for respiration through the general integument, and a repeated ability to put out neomorphic or special adaptive gills, and – in the aeoliids – to use the cerata as respiratory organs. In the nudibranchs, and to some extent in the pleurobranchs too, the development of a naked body and the clean-water habitat has to a large extent removed the need for active promotion of water currents over the gill surface. The role of the small cilia of the gill surface is simply to remove lodging particles, and to distribute mucus and possibly defensive secretions (see THOMPSON, 1960).

The Pleurocoela as a group have probably had a prolonged apprenticeship of ploughing through or burrowing into fine sediments (see MORTON, 1967). This habit is most evident today in the bullomorphs *Actaeon, Haminoea* and *Philine;* and it appears to be associated with a plicate gill and efficient pallial cleansing arrangements in the form of a strongly ciliated caecum. In the only known aplysiomorph to retain a coiled external shell, namely *Akera,* the normal habit is grazing on green algae (*Ulva* or *Enteromorpha*) from soft sediments in highly turbid water. The efficient cleansing arrangements of the mantle cavity have obviously the highest expression in species living in muddy or fine sedimented bottoms; yet in both the bullomorphs and in *Akera* the gill and caecal structure are so alike that we may safely assign them to a common ancestry within the natural group made up by the order Pleurocoela. With the aplysioid line of the order, the chief habitat has become a clean-water one for almost all members. Though some species, as the New Zealand *Bursatella glauca,* have a browsing habit on mudflats, the majority of Aplysiidae frequent algae in clean rock pools; the sole of the foot is narrowed and the whole body form re-fashioned for clinging or crawling over algae. An alternative clean water habitat for aplysioids is that adopted by the *Dolabrifera* species; these (see MILLER, 1969 for ecology) have a broad sole and depressed, streamlined body. They attach firmly to wave-swept rock-surfaces on exposed, clean-water coasts. In the Akeratidae alone among aplysiomorphs does the primitive equipment of a a pallial caecum appear.

Though the gill appears to be clearly homologous in bullomorphs and aplysiomorphs, the disposition of the plicae differs characteristically in the two groups, typified

respectively by the transversely pleated gill surface shown in *Haminoea,* and the gathering of the plicae in radiating tufts in *Akera.* The plicate gill of the Pleurocoela has no significant resemblance in detailed structure with the prosobranch ctenidium. If a distinctive name be needed for it, we could use the inclusive term "plicatidium." The branchial structures of pleurobranchs and nudibranchs are clearly diverse and different again; our present information is insufficient to press strictly their homology with the plicate gills of the pleurocoeles.

SUMMARY

A detailed description is given of the pallial organs of the primitive aplysiomorph opisthobranch *Akera bullata.* The relation of the gill is shown with the inhalant and exhalant channels, and with the purple and opaline glands. The dorsal and ventral raphe and the incipient pallial caecum have assumed the chief role of maintaining a water current through the pallial cavity. The detailed structure of the gill is compared with that of the prosobranchs, and of other molluscs with a ctenidial gill. It has fundamental differences from other molluscan gills, having neither filaments nor current-driving cilia. Its structure is that of a double fold of respiratory epithelium, thrown repeatedly into transverse folds which are in themselves minutely plicate. Respiratory water, drawn by the large strong cilia of the dorsal and ventral raphe, passes through the narrow spaces between the folds, both above and below.

The chief resemblances to the akeratid gill are found among other aplysiomorphs. Comparison is also made with the folded gill of the bullomorphs. The functions of the pallial siphon and the so-called 'adductor muscles' in tectibranchs is discussed. A comparative discussion deals with the gills of opisthobranchs in general. None of these is a true ctenidium, and they consist of a variety of special structures. Some detail is given of the structure and function of the gill of the pleurobranchomorph *Pleurobranchus membranaceus,* which is compared with the circum-anal gills of doridomorphs.

A new inclusive term for the folded gill of opisthobranchs, the word 'plicatidium' is suggested.

ACKNOWLEDGMENTS

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